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HUNTING THE HUNTERS: SPATIAL AND TEMPORAL RELATIONSHIPS OF PREDATORS THAT HUNT AT THE SAME SITES

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ABSTRACT. Newly emerged crab spiderlings *Misumena vatia* (Clerck 1757) that recruit to goldenrod *Solidago* spp. inflorescences are subject to predation by small jumping spiders (Salticidae), principal among them being middle-instar *Pelegrina insignis* (Banks 1892). I censused goldenrod inflorescences to determine whether the distribution and abundance of crab spiderlings and small jumping spiders were related to one other. The censuses demonstrated a modest negative relationship in the presence of the two species to each other on the inflorescences of goldenrod clones. On inflorescences cleared of spiders and stocked with 20 dyed crab spiderlings, a strongly negative relationship occurred between numbers of recruiting jumping spiders and crab spiderlings on the first two days, but on the third and fourth days a significant positive relationship occurred. A similar pattern occurred on clones cleared of spiders and stocked with 20 spiderlings and three jumping spiders, but the shift to a positive relationship took place after a single day. This shift in behavior apparently occurred after the spiderlings found satisfactory hiding and hunting sites. Seventeen of the 39 jumping spiders captured at these sites during the two experiments had dye on their mouthparts, indicating that they had captured crab spiderlings during this time.

Keywords: Araneae, spiders, *Misumena*, Salticidae, intraguild predation

Although ecologists have traditionally portrayed trophic relationships as simple food chains with two levels of predators, primary and top predators, it is often not appreciated that the relationship between members of these two levels may reverse itself; that is, trophic levels 3 and 4 might change to levels 4 and 3, respectively (e.g., Rypstra & Samu 2005; Morse 2006). The phenology of these species is often not in close synchrony, and thus the relative sizes and relationships of any two such species may vary greatly over time. In that some predators routinely capture prey that are extremely large relative to their own size, which species is predator and which is prey in these interactions may routinely shift over their respective life cycles. Such intraguild predation (Polis 1981) can subsequently affect not only these predators, but their herbivorous prey and, indirectly, the latter's food plants as well (Polis et al. 1989; Holt & Polis 1997; Arim & Marquet 2004).

As highly aggressive predators that hunt over their entire free-living lifetimes, during which their mass may span over three orders of magnitude, spiders present a particularly striking, though not unique, life style. Both conspecifics with slightly different emergence times and species with somewhat different phenologies, the subject of this paper, may differ in size within and between themselves at any given time. Most significantly, at certain seasons members of the smaller species may exceed the size of the larger species. Since small species often have earlier reproductive periods than larger species (Foelix 1996), this relationship is not unusual (e.g., Hodge 1999; Balfour et al. 2003; Rypstra & Samu 2005). However, it may significantly impact the behavior (see Lima & Dill 1990; Lima 1998; Morse 2006) or even the population size of the larger species, in this way lessening its impact at a point high on the trophic pyramid.

Such a relationship occurs between crab spiders *Misumena vatia* (Clerck 1757) and jumping spiders (Salticidae) that frequent flowering goldenrod (*Solidago* spp.) in the late summer (Morse 2006). When *M. vatia* spiderlings emerge from their egg sacs in July and August, they are smaller than the middle-instar (± fourth instar) jumping spiders that hunt at these sites, even though late-instar and adult *M. vatia* considerably exceed these jumping spiders in size and routinely prey on them (Morse 1992). As a consequence, although both *M. vatia* spiderlings and the jumping spiders feed on many of the same prey when in the vicinity of flowers, jumping spiders may capture *M. vatia* spiderlings in late summer and autumn. Sometimes locally abundant, *M. vatia* spiderlings may then even provide an important food source for juvenile jumping spiders, and these jumping spiders may become one of the major sources of mortality for the crab spiderlings (Morse 1992). It is therefore of considerable interest to establish whether the distribution of the two species on flowers at this time is nonrandom in relation to each other. Establishing this relationship will provide important insight into whether the presence of one species affects the distribution of the other, or whether the numbers of individuals reported in earlier studies (Morse 1992, 2006) are a mere consequence of random contacts between the two species, which may both be drawn to flowers attracting large numbers of prey insects (Morse 2000, 2005). These results have important implications for the nature and integrity of these species and for the food web in general. Here I present a series of observations and experiments that address this question.

METHODS

Site and species.—I conducted this work at the Darling Marine Center of the University of Maine, South Bristol, Lincoln County, Maine, USA, in a 3.5 ha old field surrounded by mixed coniferous-deciduous forest. The field, mown yearly in October, contains several grasses (Gramineae), and the main forbs flowering during the study period are goldenrods, asters (primarily *Aster umbellatus*) and wild carrot *Daucus carota*.

This study was confined to Canada goldenrod (*Solidago canadensis*), by far the commonest flowering species in the study area during late July and August. Canada goldenrod grows in clones that form distinct clumps in the study area. Most flowering clones contain 15–70 flowering stems of 70–100 cm height, culminating in large yellow, plume-like inflorescences with hundreds of small flower heads. Those used in this study contained 25–35 flowering stems, which I used as they reached peak flowering.

Misumena vatia spiderlings weigh 0.4–0.7 mg when they emerge from their natal nests in late summer (Morse 1993). They then move rapidly on silk lines in search of satisfactory hunting sites, usually goldenrod inflorescences, due to their ubiquity during this period and to the spiderlings' strong preferences for these flowers (Morse 2005). Throughout this paper the term "spiderling" refers exclusively to second-instar *M. vatia*. Several species of small jumping spiders, typically in their middle instars, also frequent goldenrod inflorescences in the study area. Though smaller than *M. vatia* of the same instar, and potential prey of late-instar and adult *M. vatia*, in late summer they are larger than recently emerged young *M. vatia* and readily prey on them (Morse 1992). By far the commonest of these jumping spiders is *Pelegrina* (=*Metaphidippus*) *insignis* (Banks 1892), and others include *Eris militaris* (Hentz 1845) and *Evarcha hoyi* (Peckham & Peckham 1883). All salticids used in experiments reported in this study were *P. insignis*. In a recent study at this site, *P. insignis* made up 88% of the middle-instar jumping spiders, *E. militaris* 9%, and *E. hoyi* 3% (Morse 2006).

Censuses and experiments.—I censused *M. vatia* spiderlings and jumping spiders, as well as other possible predators, on several flowering goldenrod clones. Since other possible predators were only occasionally found on these flowers (small nabid, reduviid, and phymatid bugs) I do not consider them further. I first carefully inspected each inflorescence by hand and then beat the inflorescences several times, initially gently, against a flat, hard, white surface to flush and locate any individuals not found in the initial inspection. Numbers of spiderlings and jumping spiders recorded in these censuses were compared to determine whether their numbers were correlated with each other.

I used many of the cleared goldenrod clones, randomly selected, to conduct the experiments. I placed sets of 20 *M. vatia* spiderlings, one per inflorescence, on each of 60 clones. Before releasing the spiderlings, I dusted them with fluorescent red powdered micronite dye to facilitate recapture. This treatment does not affect the behavior of the spiderlings (Morse 1993, 2000) or their vulnerability to predation (Morse 2006). One day later I censused 15 of these clones exhaustively for numbers of remaining dyed individuals and numbers of jumping spiders that had recruited to these sites. I similarly censused 15 more of these clones on days 2, 3, and 4 following the introductions.

Table 1.—Numbers of crab spiderlings (= crab) and jumping spiders (= jump) on goldenrod clones (mean ± SE). Linear regressions of numbers of the two species on individual inflorescences tested by *t*-tests (Zar 1999:336). $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$, $^{****}P < 0.0001$. Number originally on inflorescences (Day 0), numbers present one to four days after clearing of inflorescences and addition of spiderlings (Days 1–4), and numbers present one to two days after clearing of inflorescences and addition of spiderlings and jumping spiders (Days 1–2).

Spiders added	Days	Clones used	Number of crab	Number of jump	r^2	*t*
0	0	37	1.8 ± 0.35	0.9 ± 0.18	−0.22	2.14*
20 crab	1	15	6.8 ± 0.95	0.3 ± 0.21	−0.47	6.05****
20 crab	2	15	6.7 ± 1.12	0.6 ± 0.32	−0.45	4.77***
20 crab	3	15	4.9 ± 0.83	0.4 ± 0.19	+0.53	6.11****
20 crab	4	15	3.2 ± 0.56	0.4 ± 0.19	+0.32	5.52**
20 crab, 3 jump	1	10	7.1 ± 0.97	1.1 ± 0.28	−0.50	5.28***
20 crab, 3 jump	2	10	5.1 ± 1.08	0.5 ± 0.27	+0.21	4.27**

I also ran similar experiments ($n = 20$ clones) in which I introduced three jumping spiders (dyed green) at the same time as the 20 *M. vatia* spiderlings. I censused 10 of these sites after 1 day and the other 10 after 2 days.

While recording data from the experimental clones, I captured as many of the jumping spiders as possible. I examined them carefully, especially their mouthparts, under a dissecting microscope for traces of dye to determine whether they had captured any of the spiderlings, or dyed jumping spiders in the case of undyed individuals. Tests had previously established that these dyes remain on their mouthparts for up to a few days after feeding on recently marked spider or insect prey (Morse 2006). This technique thus provides a convenient method for establishing minimum rates of jumping spider predation on the spiderlings in the field. The dyeing procedure also permitted me to separate the test *M. vatia* spiderlings from any other conspecifics that might have recruited to the sites subsequent to the manipulation (whose numbers were very low).

Voucher specimens were placed in the Florida State Collection of Arthropods, Gainesville, Florida.

RESULTS

Numbers of *M. vatia* spiderlings and jumping spiders were negatively related on unmanipulated goldenrod clones (Table 1). On cleared clones seeded with spiderlings, numbers of spiderlings and recruiting jumping spiders were initially strongly negatively correlated (days 1 and 2), but then suddenly became strongly positively correlated on days 3 and 4 (Table 1). A similar pattern held on the clones seeded with both spiderlings and jumping spiders; however, the transition on these clones occurred after only 1 day rather than 2 days (Table 1).

Where only spiderlings were added to the clones, there was no relationship over the four-day period between the number of jumping spiders present and whether the relationship between the two groups was negative or positive (Table 1). Jumping spiders recruited to these sites rapidly, such that their numbers (means = 0.3–0.6 per clone; totals of 5–9 individuals in 15 clones) were rather similar in each of these samples. In contrast, in the clones to which jumping spiders were added, their numbers were considerably higher on day 1 than in the clones to which only spiderlings were added. However, on day 2, numbers of jumping spiders on the "seeded" sites were similar to numbers at sites to which only spiderlings were added (Table 1).

Free-ranging spiderlings exhibited a strongly clumped distribution. Many fewer singletons and pairs and many more vacant sites occurred than predicted by chance in a Poisson distribution (Fig. 1: $G = 102.05$, $df = 3$, $P < 0.001$ in a *G*-test for goodness of fit).

Free-ranging jumping spiders at the census sites were also not randomly distributed when compared with a Poisson distribution (Fig. 2): $G = 22.29$, $df = 2$, $P < 0.001$ in a *G*-test for goodness of fit). They exhibited fewer ones and twos, and more zeros and threes, than predicted from a Poisson distribution. A particularly striking result was the abrupt drop-off between threes and fours, a factor that could not be

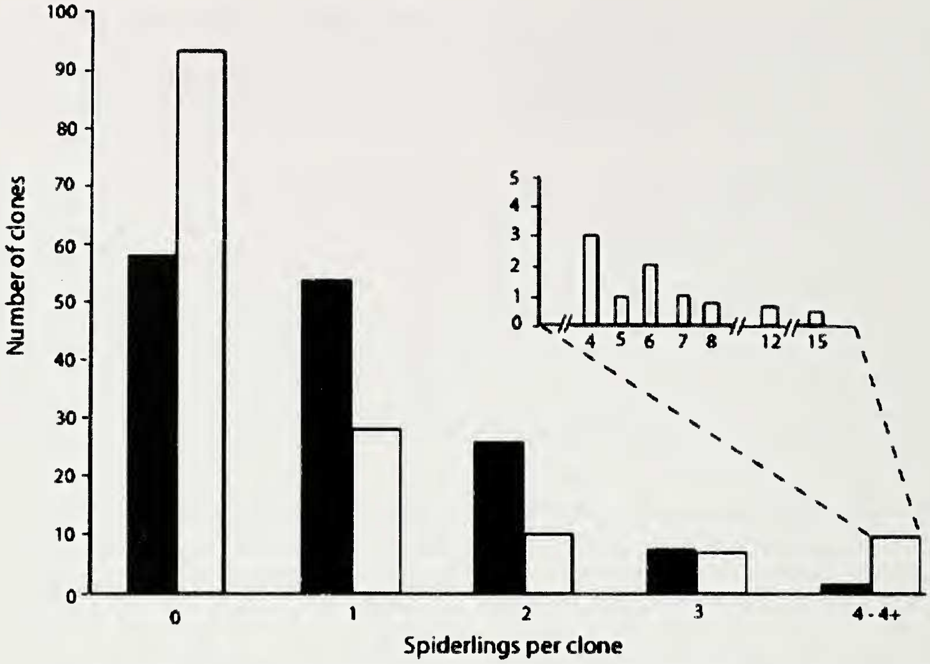

Figure 1.—Expected (black bars) and observed (white bars) numbers of *Misumena vatia* spiderlings on goldenrod clones, $n = 146$. Expected numbers based on a Poisson distribution. Inset details numbers of clones containing four or more spiderlings. Axis labels for insert are same as major figure.

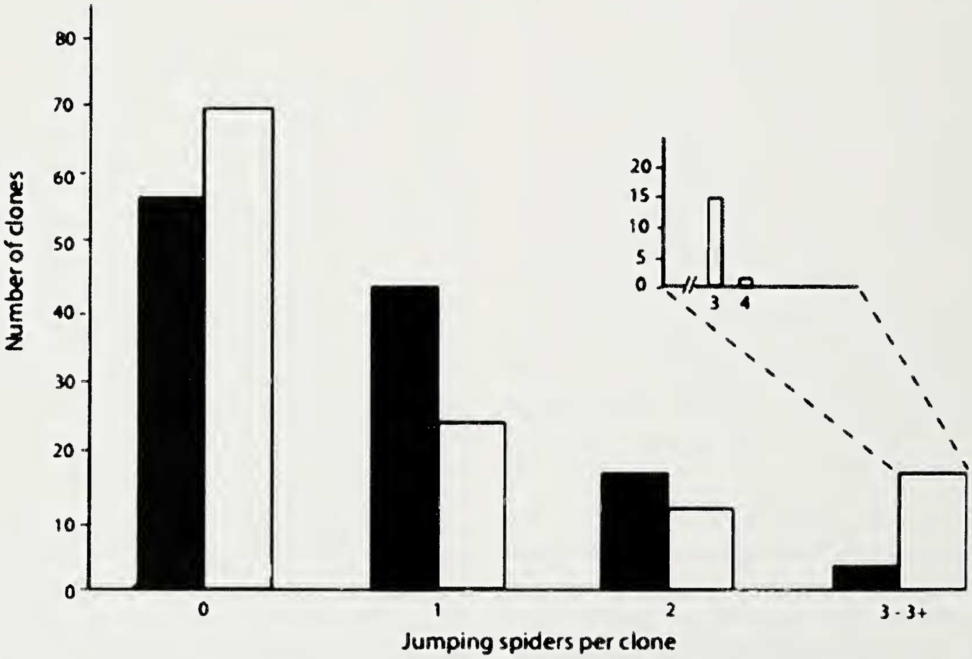

Figure 2.—Expected (black bars) and observed (white bars) numbers of jumping spiders on goldenrod clones, $n = 122$. (n does not match that of Figure 1 because data for jumping spiders were inadvertently not gathered at 24 clones.) Expected numbers based on a Poisson distribution. Inset details numbers of clones containing three or more jumping spiders. Axis labels for insert are same as major figure.

explicitly incorporated into the test for significance due to the small expected number of individuals at those densities.

In the analysis of the jumping spiders captured on the goldenrod clones, 17 of the 39 individuals (43.6%) examined contained pink dye about their mouthparts, highly suggestive of significant predation on the experimental *M. vatia* spiderlings. Only a minority of marked jumping spiders was recorded in subsequent censuses (27.3%, $n = 32$).

DISCUSSION

The free-ranging spiderlings showed a weak avoidance of the clones occupied by jumping spiders, and they exhibited a strong tendency for clumping, probably a consequence of limited dispersal from their natal sites. Many of the spiderlings were concentrated at a few sites, probably members of broods that had very recently left their natal sites. Thus, the patchiness of the spiderlings doubtlessly had a strong temporal aspect to it. The abrupt drop-off in numbers of jumping spiders after they reached a density of three per clone is consistent with a density-dependent effect limiting their numbers within these sites. As cursorial predators they probably frequently encounter each other and thus quickly attain an accurate estimate of their densities.

The experiments showed an initial strong negative relationship between the spiderlings and the jumping spiders, followed by a strongly positive relationship. This distribution is consistent with the spiderlings initially avoiding the jumping spiders, either as a consequence of direct contact with the jumping spiders or possibly with their silk. Alternatively, this relationship could result from the jumping spiders capturing the spiderlings. Spiderlings flee when in near or direct contact with jumping spiders, which readily capture them when given the opportunity (Morse 2006). Other *M. vatia* life stages respond negatively to some draglines encountered (Leonard & Morse 2006), and spiderlings might have that ability as well, though I have not tested for it.

Surprisingly, the relationship between the spiderlings and jumping spiders subsequently suddenly became strongly positive. This relationship occurred after two days in the experiment without addition of jumping spiders but after only one day in the experiment with jumping spiders added. The positive relationship seems most likely to be a similar response by both species to the substrate or to small dipteran prey. The shift in distribution could be in part a consequence of the spiderlings acclimating to the jumping spiders. Once they have located satisfactory hunting sites, the spiderlings become relatively sedentary and conceal themselves within the flower heads of the inflorescences, thereby greatly lowering their vulnerability to the jumping spiders (Morse 2006). Although one might suspect that the change in distribution resulted from a decrease in the number of jumping spiders, the jumping spiders' numbers remained relatively constant over the experiments in which none of them were added. In the experiments in which marked jumping spiders were added, relatively few of those subsequently captured or sighted were marked individuals, suggesting that the population of jumping spiders on these inflorescences is large and dynamic, with members constantly entering and leaving the clones.

Thus, these results suggest a negative relationship between the two spiders that is alleviated by the spiderlings eventually finding satisfactory hunting sites. The jumping spiders likely have an even stronger effect on this relationship when they contact the spiderlings than is suggested by the results from the censuses. Observations of these interactions demonstrated that jumping spiders would typically quit a clone before searching all of the inflorescences and that they often did not find ensconced spiderlings on inflorescences that they did search. However, when they did find spiderlings, the results were pronounced—several spiderlings were captured, and the escape responses of others were striking. Escaping spiderlings quickly descended from their sites on silk lines and sprinted off into the litter (Morse 2006). Although these data suggest a low level of search activity on the part of the jumping spiders at any given time, given their strong perceptual abilities (Jackson & Pollard 1996) and the density of the spiderlings, they could be pursuing an optimal search pattern.

The tables were turned in the relationships between adult *M. vatia* and the jumping spiders in which the adults readily attacked and captured the jumping spiders (Morse 1992). Rypstra & Samu (2005) described an analogous relationship between two species of wolf spider (Lycosidae) in which late instars or adults of

Pardosa milvina (Hentz 1844) (adults = ca. 20 mg) were in regular contact with early instars of *Hogna helluo* (Walckenaer 1837) (adults = ca. 800 mg). Under these circumstances, older individuals of the small species routinely attacked the early instars of the large species, whereas most instars of *H. helluo* preyed upon *P. milvina*. Such relationships are probably not unusual.

These fluctuating relationships between major participants in the plant-pollinator system have interesting potential consequences for the organization of their communities. The jumping spiders presumably lower the impact of the crab spiderlings, which in turn take large numbers of small flies that probably function as nectar robbers (Morse 2005). The jumping spiders themselves probably capture many more small flies than they do spiderlings. It remains to be seen whether these interactions play an important role in the evolution of plant-insect relationships on goldenrods, old-field dominants. Observations suggest that in some years, numbers of *M. vatia* spiderlings in the study area are more likely to be driven by herbivores that impact the abundance of the goldenrods (bottom-up effects) (Carson & Root 2000; Morse 2007) than by predators such as small jumping spiders (top-down effects).

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